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The Role of Microbial Dispersal in Overcoming Factors that Constrain Soil Respiration Response to Climate Change

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The Role of Microbial Dispersal in Overcoming Factors that Constrain Soil Respiration Response to Climate Change

by

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Thesis

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Master of Arts

The University of Texas at Austin

December 2018

Acknowledgements

I would like to thank Jetton Fontenot, Brianna Barry, Brian Aiken, and Alex Aguirre for assistance with fieldwork and labwork. Hannah Giauque, Elise Worchel, Colin Averill, and Stephanie Kivlin also provided assistance and a sounding board at various points during the course of the experiment and analysis. Site access was kindly permitted by the Texas Parks and Wildlife Department and the Texas Ecolab Program. Funding was provided by a National Science Foundation RAPID program award to CVH (DEB-1546740) and Texas Ecolab funding to CVH.

Abstract

The Role of Microbial Dispersal in Overcoming Factors that Constrain Soil Respiration Response to Climate Change

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The University of Texas at Austin, 2018

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The largest remaining uncertainty in the terrestrial carbon cycle is whether soil will become a carbon source or sink in future decades. Better ecological understanding of the soil microbial communities that regulate soil respiration and carbon decomposition can improve parameterization of global carbon models. Here we investigate whether climatic legacy effects, which can constrain microbial function in the face of environmental change, can be overcome by effective dispersal. To address this gap in knowledge, we performed a lab microcosm experiment using 15 combinations of soil communities to mimic potential dispersal outcomes and maintained these under wet or dry conditions. Soils were taken from three sites at the drier western and three sites at the wetter eastern ends of a precipitation gradient in central Texas with a similar geomorphic profile and known legacies dependent on historical rainfall. Soil origin treatment was created from two western sites, two eastern sites, or a mixture of one western and one eastern site. Dispersal treatment was based on the amount of each soil origin in the mixtures (0:100, 15:85, 50:50, 85:15, 100:0).

The mixtures were created by adding live soil inoculum (2.5 g) to autoclaved background soil (22.5 g) comprised of a mixture of soils from all six sites. We assessed whether changes in soil respiration were due to moisture regime or dispersal treatments over 12 weeks. Contemporary soil moisture was the primary driver of respiration, with 878% more respiration in wet vs. dry treatments. Soils that were evenly mixed western communities differed from the other soil dispersal treatments, likely because of intrinsic functional limitations or increased biotic interactions. Legacy effects were substantially weaker here compared to other studies in the same system. We speculated that the resources provided by autoclaved background soils might have disrupted the historical contingency of soil moisture in this system. Community composition data must be used to resolve whether the lack of functional differences were due to microbial communities sharing similar taxa or physiological plasticity between differing communities.

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INTRODUCTION

The soil microbial community contributes to the global carbon cycle primarily by affecting the balance of respiration and the storage of soil organic matter (Trumbore, 2006). The annual carbon flux between the Earth's soils and atmosphere is at least an order of magnitude greater than the carbon released by anthropogenic fossil fuel combustion, approximately 60 gigatons (Giardina, Litton, Crow, & Asner, 2014). Estimating the direct contribution of soil microbes to overall soil respiration on a global scale has proven challenging, but values at the ecosystem level range from 36-84% of total soil respiration (Cisneros-Dozal, Trumbore, & Hanson, 2006). Understanding how the feedbacks of altered environmental drivers such as temperature, nutrients, and moisture interact with soil carbon dynamics is critical for modeling climate change impacts and crafting appropriate responses (Crowther et al., 2016). Current ecosystem models that predict whether soil will become a net source or sink of CO2 assume that microbial communities regulating decomposition will maintain their function in the face of environmental change, known as rapid acclimatization (Todd-Brown, Hopkins, Kivlin, Talbot, & Allison, 2011), and may be an outgrowth of previous thinking that held that microbial distribution was ubiquitous (Fenchel, 1993). Previous work including some in our study system has instead found evidence that microbial function is driven by historical climate conditions more than current conditions (Andersson, Berga, Lindstrom, & Langenheder, 2014; Averill, Waring, & Hawkes, 2016; Bond-Lamberty et al., 2016; Hawkes, Waring, Rocca, & Kivlin, 2017; Waring & Hawkes, 2018).

Rapid acclimatization can occur through several microbial mechanisms, including physiological plasticity and community shifts (Cregger, Sanders, Dunn, & Classen, 2014). Physiological plasticity permits a given microbial community to respond to changing environmental drivers without disrupting function, and is understood in the context of neutral theory that holds that there is a large amount of functional redundancy between

taxa (Hubbell, 2001). Székely et al. (2013) found that community composition of aquatic microbial communities subject to experimental mixing maintained a strong signal of the source community despite differing salinity environments. In soils, physiological shifts were more important than community composition in controlling carbon mineralization responses to experimental moisture regimes, further supporting the idea that functional plasticity is an important element in microbial response to environmental change (Kaisermann et al., 2015).

Acclimatization via community shifts occurs when different taxa predominate under different environmental conditions, which may result from internal turnover or dispersal (Lennon, Aanderud, Lehmkuhl, & Schoolmaster, 2012). Internal shifts in taxa are expected to occur when the environment changes, with changes in relative abundance of the active portion of the community or transitions between dormant and active taxa (Fodelianakis et al., 2017; Kaisermann et al., 2017). Microbial community composition is known to respond to climate factors in the absence of dispersal, including both moisture and temperature (Clark et al., 2009; Evans & Wallenstein, 2014; Meisner et al., 2018; Rousk et al., 2013). Notably, shifts often depend on specific functional groups within the community (Castro, Classen, Austin, Norby, & Schadt, 2010; Whitaker et al., 2014). For example, Castro et al. (2010) determined that changes in precipitation regime led to increased abundance of Proteobacteria in wet treatments, and more Acidobacteria in dry treatments. Nevertheless, in natural systems, dispersal from outside the local community is expected to be less important than natural turnover, except potentially in the face of major disturbance(Nemergut et al., 2013).

Species sorting by environment via dispersal can rescue function in the face of an environmental shift by allowing taxa that are well adapted to the new conditions to dominate the community over a relatively short period of time (Van der Gucht et al., 2007). Thus, dispersal may be particularly important where local functional specialization occurs in the microbial community, limiting intrinsic plasticity or

functional breadth. However, in bacterial communities from lakes in the Netherlands, high dispersal was necessary to alter overall community structure (Lindström & Östman, 2011). Other studies of aquatic microbial systems support dispersal as a mechanism for functional adaptation to a changing environment (Comte, Langenheder, Berga, & Lindstrï¿½m, 2017; Székely, Berga, & Langenheder, 2013). In soil microbial systems, there is experimental evidence both for taxa which are not dispersal limited, such as fungi with airborne spores, where deterministic filtering either via edaphic variables or biotic interactions structures the community (Kivlin, Winston, Goulden, & Treseder, 2014), and against: ectomycorrhizal fungi which also produce large numbers of airborne spores did demonstrate dispersal limitation in a tree island setting in California (Peay, Garbelotto, & Bruns, 2010). A modeling approach (Evans et al., 2017) concluded that dispersal interacts with the environment to structure community composition and potentially function, but the level of dispersal must be over a certain threshold for the effects to be significant. Theoretical approaches have held however that dispersal at high levels may lead to greater abundance of taxa that are locally maladapted, so increased dispersal could lead to a mismatch between function and environmental conditions (Graham, 2017; Leibold, Chase, & Ernest, 2017).

If physiological plasticity is lacking and dispersal is limited or ineffective, then microbial function may be constrained by past conditions (Hawkes & Keitt, 2015; Ogle et al., 2014). If such legacy effects are persistent over relevant time scales, then incorporating the presence or absence of legacy effects into microbial parameters has the potential to increase the accuracy of ecosystem biogeochemical models (Treseder et al., 2011). Current evidence is equivocal for climate legacies in soil microbial communities from sites where temperature and rainfall have been experimentally manipulated. For instance, moisture history structured nitrous oxide emissions in agricultural fields (Banerjee et al., 2016) as well as respiration and community composition in soils influenced by an 11-year drought treatment in semi-arid grasslands

(Evans & Wallenstein, 2014). In contrast, historical legacies were not found in a warming and drought experiment imposed for 10-13 years in mesic European environments (Rousk et al., 2013). Legacies can vary for different processes in the same system; for example, in a wetland mesocosm experiment nitrification rates were influenced by moisture history while denitrification rates were not (Peralta, Ludmer, & Kent, 2013). Understanding the drivers of legacies and how they might be overcome will determine whether soil microbial processes can be generalized accurately across sites.

Previous soil microbial community research along the Edwards Plateau in Central Texas has established the presence of a legacy effect which corresponds to historical rainfall (Averill et al., 2016; Hawkes et al., 2017; Waring and Hawkes, 2018). Moisture has long been known to be an important element of microbial functioning (Kieft et al., 1993). Soil respiration both in the field and in laboratory experiments (Waring & Hawkes 2018) was always greater for soils originating from the wetter, eastern side of the Edwards Plateau precipitation gradient. Soils from drier sites, in contrast had lower maximum respiration rates at low and high moisture levels. Moreover, these historical contingencies appeared to be unaffected by dispersal, whether in the form of passive dispersal into open cores or direct inoculation (Waring and Hawkes 2018). However, it is possible that the dispersal treatments were ineffective in allowing establishment due to severe drought at the time or to the small amounts of filtered inoculum that were applied (Waring and Hawkes 2018, Yan et al., 2014). Thus, the role of dispersal as a mechanism for overcoming historical contingencies remains an open question in this system.

Our objective was to examine whether microbial dispersal can overcome local climate legacies in controlling microbial community functional responses to moisture. We hypothesized that forcing effective dispersal by mixing soil microbial communities from sites with similar geological history but differing precipitation regimes would release microbial communities from climate-driven legacy effects (Hypothesis 1).

Additionally, we hypothesized that lower dispersal levels would not shift functional response to moisture changes unless species sorting to moisture was the primary driver (Hypothesis 2). To test these ideas, we manipulated dispersal in soils collected from a rainfall gradient in lab microcosms. Sites with either the same or different rain histories were mixed pairwise in three different proportions, along with single site controls. Microcosms were maintained at either high or low soil moisture to mimic the ends of the rain gradient, and carbon respiration was measured over a three-month period.

METHODS

Experimental Design

To test the how climate history and dispersal affect soil respiration under altered moisture regimes, we used lab microcosms (Figure 1) to create soil microbial communities with three treatments: (1) soil origin across a rain gradient (drier west vs. wetter east), (2) proportion of each soil origin mixtures (0, 15, 50, 85, 100%), and (3) water treatment (5% [dry] or 20% [wet] soil moisture). The full experimental design included fifteen possible site combinations, five levels of dispersal treatment, and two levels of moisture in a full factorial design. With four replicates and 8 blanks, the total number of vials was 608 (Figure 2). Respiration was measured every two weeks over 10 weeks (n=5 measurement dates), after allowing the microcosms to establish themselves for 2 weeks for a total duration of 12 weeks. Microbial biomass was measured from samples taken from each microcosm at the end of the twelve-week period. Each of these treatments is described in more detail below.

Field Soil Collection and Site Description

Soils were collected from the Edwards Plateau in central Texas, where a steep rain gradient of 400-900 mm mean annual precipitation (MAP) spans ~400 km. Soils were collected in June 2014 and June 2015 from three sites in the western end of the gradient with 442-602 mm MAP and three sites in the eastern end of the gradient with 812-889 mm MAP (Table 1; for further site description, see Hawkes et al. 2017, Averill et al. 2016).

Soils were collected from two 400-m^2 areas of each site where grass made up at least 50% of the vegetative cover and slope was < 5%. Soils were sampled at random locations so long as they were at least a meter apart across the plot, to a depth of 10 cm using a trowel. Soils were sieved to 1 cm in the field to remove large rocks and stored in plastic bags in a cooler on ice for transport to the laboratory where they were sieved to

2 mm and air-dried to 5% moisture. The 2014 soils were stored at room temperature in plastic bags for 13 months. The 2015 soils were used immediately for the microcosms.

Microcosms and Treatments

The microcosms were constructed of 60-mL borosilicate glass tubes (manufactured by I-CHEM) with a septa cap. Each tube was filled with 22.5 g of "background" soil and 2.5 g of treatment soil. Background soil consisted of soils collected from the six sites in 2014 in equal proportion. Background soil was autoclaved three times at 121 °C for 1 h over 3 days with 24-h intervals.

Treatment soil consisted of air-dried soils collected from the field sites in 2015. Treatment soils were added as combinations of two eastern sites, two western sites, or one eastern and one western site in five different ratios (100:0, 85:15, 50:50, 15:85, or 0:100). The set of dispersal treatment mixtures that were 100% from a single site, either the east or west end of the Edwards Plateau precipitation gradient were created to be able to assess whether the environmental legacy effect was present in our microcosm-based experiment. We also included 8 blanks, which consisted of 25 g of background matrix soil with no treatment soil inoculant, to monitor the base level of respiration of taxa that potentially survived sterilization or were established post-sterilization. The site combinations are shown in Figure 2. In this way we examined the mixed communities versus each of the origin communities on their own, as well as whether the effect of each community in the mixture depended on its presence or abundance.

Soil moisture treatments were 5% and 20%, representing the low and high end of precipitation along the gradient. Moisture treatments were maintained weekly by weight with sterile water. To prevent excessive water loss to air but allow for gas exchange, vials were sealed between handling periods with parafilm.

Respiration

We measured respiration by sealing the vials with rubber septa caps, flushing the airspace with CO_2-free air, allowing respiration to proceed for an hour, then sampling the headspace inside the vial with a syringe. Headspace samples of 14 mL were transferred to a previously evacuated 12-mL vial with a rubber septa cap for storage. CO_2 in the headspace samples was quantified on a gas chromatograph with a FID detector and a methanizer (SRI Instruments, Torrance, CA, USA). For each sampling date, evacuated vials were created with standard carbon dioxide values so microcosm samples could be quantified and to provide a correction factor for any leaking the vials may have experienced over the storage period. The CO_2 concentrations were corrected for carbon dioxide present after flushing the headspace of blank vials (with room air sent through a CO_2 scrubber) and subsequently were converted to flux rates (μg CO2 g-1 h-1).

Microbial Biomass

After the last gas sampling point, 5 g of soil from each microcosm was mixed in 25 mL 0.5M K2SO4 to extract DOC, and a separate 5 g sample of soil was fumigated overnight with $CHCl_3$ and then extracted to provide DOC plus microbial Carbon (Vance et al., 1987). We stored extracts at -20 °C prior to colorimetric analysis of organic carbon following Giasson et al. (2014) with the following changes to optimize for local soils. Soil concentrations below 0.25 mM C were not distinguishable by this method, so all samples below that threshold were assigned a value of 0.25 mM C. The values resulting from the assay were then converted to per gram of dry soil to obtain mass of microbial carbon per gram of dry soil.

Statistical Analysis

We tested for legacy effect by analyzing the respiration data for only the single site communities (100:0 and 0:100 mixture proportions). We constructed a linear model

with the lm package (R Core Team, 2014) with factors of origin (east or west), soil moisture (5% or 20%), and their interaction. The model was tested for significance ($P < 0.05$) with Type III SS in the Anova function in the R car package (Fox and Weisberg, 2011)

For all treatments, average respiration across the total duration of the experiment was tested with a linear mixed model constructed in R's lmerTest package (Kuznetsova et al., 2017). Fixed effects were soil moisture, dispersal treatment, and origin. Site combinations were a random effect. All fixed effects that were significant at $P < 0.05$ with the lmerTest model output were run through a posthoc analysis with the Anova and emmeans packages. All significant interactions were investigated by running a one-way ANOVA on each level of a factor across the levels of the other factor involved in the interaction, with a post hoc pairwise Tukey HSD test using the R package emmeans (Lenth 2018). Microbial biomass was analyzed using the same model as average respiration.

All statistical analyses were conducted in R v. 3.3.2. Graphical figures were constructed in R using the packages ggplot2 and cowplot (Wickham 2016, Wilke 2018).

RESULTS

The microcosms consisting of the single site eastern and single site western respired in a significantly different manner by moisture level (Table 2). Respiration also tended to differ by soil microbial community origin, but this was not significant (P = 0.09) and there was no interaction of moisture and origin (Table 2) (Figure 3).

For the full dataset, contemporary moisture was the primary factor driving soil respiration (Table 3). Soils in the high moisture treatment respired 878% more than those in the low moisture treatment on average, and there were no significant interactions of moisture with other factors (Table 3, Figure 4). Soil respiration was also affected by soil origin and the interaction of soil origin with dispersal treatment (Table 3). The west-west sites had the lowest respiration rates (Figure 4). However, this origin effect was largely driven by the 50:50 combinations of west-west soil communities having significantly lower respiration at high moisture (mean = 8.042 μg CO2 g-1 h-1, range 3.175-16.412) than the other mixture combinations (mean = 12.369 μg CO2 g-1 h-1, range 3.765-28.300).

Microbial biomass C did not differ significantly on the basis of moisture, origin, or dispersal treatment (Table 4). In addition, microbial biomass C had no relationship to C respired from soils based on inclusion as covariate in the analysis of respiration (not shown).

DISCUSSION

There are differences in the respiration of soil microbial communities that depend upon climate history; however, the strength of these effects was disrupted by disassociating soil microbes from their home soils. Although moisture remained a primary driver of respiration, both dispersal and origin effects were limited. It is likely that the treatments did not behave as expected to create mixed communities and that the experimental design removed some historical constraints.

We did not observe significant differences in average respiration between the east-east and east-west soil microcosms, suggesting that the eastern origin soil microbial communities dominate in any mixture with western origin soils. Thus, effective dispersal of eastern microbes to western sites can release those microbial communities from functional constraints arising from historical contingencies assuming an increase in moisture in the future (Hypothesis 1). However, the reverse was not true – western soils did not dominate effects under dry conditions when mixed with eastern soils. Because future conditions in Texas are expected to be hotter and drier with more frequent extreme events (IPCC 2014, Jiang & Yang, 2012), we might expect historical legacies to persist.

If microbes from drier sites cannot establish well in formerly wet sites due to non-climate factors, physiological plasticity or internal shifts in community composition may play a more important role in the resulting functional response as has been seen in studies focused on response to experimental warming. Little is known about the moisture sensitivity of microbial respiration and decomposition, with various mathematical functions used in different soil carbon models (Sierra et al. 2015). In response to warming temperature, however, microbial respiration typically increases with soil temperature as a result of plasticity and rapid turnover (Hicks Pries, Castanha, Porras, & Torn, 2017; Karhu et al., 2014; Noh et al., 2016; Schindlbacher, Schnecker, Takriti, Borken, & Wanek, 2015). However, respiration often returns to the previous rate

(Carey et al., 2016), perhaps due to limiting factors such as labile carbon (Hartley, Heinemeyer, & Ineson, 2007; Melillo et al., 2002) or thermal adaptation of microbes (Crowther & Bradford, 2013; Feng et al., 2017), and the overall pattern resembles a Gaussian distribution. Soil microbial respiration will likely decrease as soil moisture decreases and precipitation variability increases, and may (or may not) recover to previous levels as temperature does depending on both other climatic variables and biotic interactions. However, both the shape of those responses and the plasticity of moisture sensitivity remain an open question (Sierra et al. 2015) as do the potential interactions of increased temperatures and lower soil moisture (Helmuth et al., 2014; Luo et al., 2016).

One possibility is that the result of mixing is affected by the balance of generalist and specialist taxa in western and eastern sites (Graham 2017, Lennon et al. 2012, Hawkes and Keitt); but Waring et al. (2018) found that most taxa were generalists across this gradient after 18 months in a reciprocal transplant experiment. Alternatively, community coalescence theory broadly posits that when whole communities are mixed together, the resultant species mix will be asymmetrical assemblies dominated by one community (Gilpin, 1994; Livingston, Jiang, Fox, & Leibold, 2014). Although environmental filtering is usually presumed to be an important element in determining which community will succeed (Rillig et al., 2015), species assemblies that have less constrained evolutionary histories are likely to dominate during community mixing, which in this case would result in eastern communities overtaking western communities in mixes (Yoshida & Tokita, 2015).

Origin also interacted with the microbial dispersal treatment; the west-west soil communities that were evenly dispersed had a significantly lower functional response than the single site communities or the asymmetrically mixed communities. These context-dependent results mean that our expectation of dose-dependent dispersal responses was not realized (Hypothesis 2). Nevertheless, this result is also consistent

with coalescent theory, in which the west-west origin mixtures must contend with functional limitations on respiration because the species inhabit narrower niche spaces than their eastern counterparts.

Although little is known about dispersal of soil microbes, the soil communities we mixed likely already experience and are resilient to moderate amounts of dispersal across this 400-km gradient, except in the most arid communities. Distance decay relationships, in which communities that are further apart are less similar than those that are closer together (Martiny et al. 2006), suggest that dispersal limitation may be common at scales greater than 1 km (Adams, Miletto, Taylor, & Bruns, 2013; Peay et al., 2010). However, Kivlin et al. (2014) confirmed that airborne fungal distributions in a California mountain range were neutrally dispersed, but that soil and physiological factors played a large role in structuring the overall soil fungal community. Effective dispersal is currently a hotly debated topic: even global studies of arbuscular mycorrhizal fungi (with their larger size spore) disagree on the contribution of dispersal to current biogeographic patterns (Davison et al., 2015; Kivlin et al., 2014; Rodríguez-Echeverrá et al., 2017)

Surprisingly, we did not observe strong legacy effects in this experiment, as we had expected. However, this is the first experiment in this system that decoupled microbes from their native soils and subjected all microbes to the same enriched resources generated by autoclaving background soils. Autoclaving has been demonstrated to increase soil carbon and nutrients by breaking up soil aggregates and through the death of microbial inhabitants (Endlweber & Scheu, 2006; Salonius, Robinson, & Chase, 1967; Serrasolsas & Khanna, 1995). Since carbon sources would have been similar across all treatments, response to labile carbon may have overwhelmed any prior moisture selection effects (Wang et al., 2013). Our results are consistent with such carbon priming (Figure 5), with a large initial respiration response that tails off over weeks (Liu et al., 2017). Similarly, both Serrasolsas et al. (1995) and

Salonius et al. (1967) observed high initial microbial respiration tailing off over a period of weeks, lending credence to the idea that substrate availability is driving the patterns seen in our study.

Legacy effects that constrain microbial community function have been observed in this system previously, as well as other systems structured specifically by a moisture legacy (Averill et al. 2016, Hawkes et al., 2017, Waring et al., 2018, Banerjee et al., 2016; Cavagnaro, 2016; Meisner et al., 2018; Peralta et al., 2013). However, microbial climate legacies have not been found in other systems (Baker, Khalili, Martiny, & Allison, 2018; Rousk et al., 2013; Schindlbacher et al., 2015; Tiemann & Billings, 2011). One possibility is that climate legacies may only occur in ecosystems where climate has been a strong selective factor. In other cases, soil resources (Marschner, Hatam, & Cavagnaro, 2015; Sinsabaugh et al., 2015; Troxler et al., 2012), disturbance (Aanderud, Jones, Schoolmaster, Fierer, & Lennon, 2013; Atlas, Horowitz, Krichevsky, & Bej, 1991; Ferrenberg, Reed, & Belnap, 2015), or elevation or pedogenic gradients (Han, Wang, Sun, Hu, & Feng, 2018; Sánchez-Marañón et al., 2017) may be more important drivers. Here, autoclaving background soils may have acted as an environmental perturbation serious enough to alter the expected soil respiration response (Göransson, Godbold, Jones, & Rousk, 2013; Manzoni, Schimel, & Porporato, 2012; Serrasolsas & Khanna, 1995).

Decoupling microbes from their natural environment has been extensively tested by reciprocal transplant experiments, where soil microbial communities are moved from their local condition (“home”) to a new condition (“away”). If there is local adaptation, communities should show maximum function in their home habitat compared to any other away habitat (Ayres, Steltzer, Berg, & Wall, 2009). For example, microbial litter decomposition was on average 7.5% faster at home than away based on a global analysis of 125 experiments in 35 studies (Veen, Freschet, Ordonez, & Wardle, 2015). In some cases, communities and function shift rapidly to match transplant

environments. Shifts are more common when the away climate is outside previously experienced conditions such as soil cores transplanted along an elevation gradient in alpine environment (Rui et al., 2015), or having an oak community shift to be like a grassland community (Waldrop & Firestone, 2006). In cases where community persists despite transplant this appears to be due to similar environmental drivers between the home and away environments, as in similar salt marshes over several months (Angermeyer, Crosby, & Huber, 2018), the same Waldrop and Firestone study where the grassland cores did not shift towards the oak communities during the transplant, and a semi-arid mountainous region of southeastern Washington over 17 years (Bond-Lamberty et al., 2016). However, the same Bond-Lamberty et al. study had large functional differences, with the more arid soils having lower function much like the 50:50 west-west soil combination in this experiment, suggesting that more arid soil microbial communities may have intrinsic limits on adaptation to more favorable conditions. Conversely, a study across a large swath of China inadvertently revealed that carbon inputs in the form of maize cropping dampened the effect of soil transplantation (Liu et al., 2014); a similar process may be taking place with increased carbon availability in autoclaved soils suppressing differences between the less constrained soil community dispersal treatments.

This study has several caveats that limit interpretation. The soil biogeochemical measurements were only taken on individual soils at the time of field sampling, prior to the beginning of the experiment. Although the relatively enhanced resource richness of the post-autoclaving microcosm environment compared to the field sites is a logical assumption, no measurements were made on the homogenized background matrix soil after autoclaving. Background soils were homogenized prior to disbursing in microcosms, but we did not explicitly control soil carbon or nutrients so we can only speculate that that was what distinguished our study from previous ones testing for legacy effects along the Edwards Plateau precipitation gradient. In addition, we analyzed

average respiration and ignored likely effects that varied across dates (Göransson et al., 2013; Hawkes et al., 2017; Zhou, Hui, & Shen, 2014). Finally, we speculate about underlying microbial community patterns that might drive the observed functional responses, but a true accounting of how forced dispersal interacts with community function will rely on sequencing of microbial community composition.

We explored whether microbial dispersal could overcome historical contingencies caused by previous climate (Hawkes et al., 2017; Waring & Hawkes, 2018). Although the effects of dispersal and climate origin were limited, we conclude that this was due to decoupling of microbes from their home soils by the experimental manipulation of background soil and soil resources. To continue work on the extent that plasticity or dispersal will lead to predictable outcomes of overall soil carbon dynamics, manipulating soil nutrients and organic matter explicitly along with moisture and soil origin would illuminate the gaps in this study. A more complete understanding of how community structure affects function could allow for better modeling of the overall soil microbial response to climate change, in particular by resolving whether soil will be a source or sink of carbon in coming decades.

Table 1 Site Description

Description of the gradient sites that were sampled for homogenized background matrix soil in 2014 and for live inoculum in 2015. Nitrate (NO_3), ammonium (NH_4), phosphorus (P), and microbial biomass carbon (MBC) values are presented for both soils collected in summer of 2014 (first row) and summer of 2015 (second row). Organic matter (% OM) is from 2014 only. The mean annual precipitation (MAP), maximum annual temperature (T max), minimum annual temperature (T min), and elevation data were obtained from Oregon State University's PRISM 30 year (1981-2010) climate dataset (http://prism.oregonstate.edu).

Site	Site Code	Lat.	Lon.	MAP (mm)	T max (°C)	T min (°C)	Elev (m)	pH	OM (%)	MBC (mM C g^{-1})	P (µg g^{-1})	NH_4 (µg g^{-1})	NO_3 (µg g^{-1})
ING Ecolab	ING	30.32	-98.44	812.19	25.9	12.5	362	6.58	2.39	16.25	0.619	0.594	0.559
								7.98		19.22	0.542	0.580	0.344
HAN Ecolab	HAN	3021	-97.96	889.24	25.9	13	346	8.19	4.99	17.83	0.045	0.703	0.921
								8.14		53.85	0.065	0.343	0.283
COL Ecolab	COL	30.32	-98.43	814.17	25.8	12.5	369	8.14	3.17	16.17	0.208	0.515	1.716
								7.97		59.17	1.247	1.149	0.624
Devils River State Natural Area	DRI	29.93	-100.92	533.63	26.9	12.7	525	8.39	2.36	30.13	0.298	0.234	1.319
								7.77		30.80	0.266	0.103	0.128
Kickapoo Caverns State Park	KCA	29.61	-100.45	602.66	26.5	13	541	8.16	4.20	64.52	0.397	3.221	1.137
								8.12		22.86	0.123	0.563	0.360
Seminole Canyon State Park	SCA	29.69	-101.31	442.33	27.5	13.9	403	7.96	5.74	66.4	0.441	0.498	7.361
								8.19		6.34	0.375	0.187	0.162

Table 2 ANOVA results for legacy respiration linear model

Analysis of Variance Table (Type III) for the legacy linear model: Average Respiration ~ Moisture + Origin + Moisture*Origin. Factors significant at $P < 0.05$ are in bold.

	Sum Sq	Df	F Value	Pr(>F)
Intercept	9620.4	1	407.821	**<0.001**
Origin	68.4	1	2.901	0.0900
Moisture	3901.7	1	165.396	**<0.001**
Origin:Moisture	46.9	1	1.986	0.160

Table 3 ANOVA results for full respiration linear mixed model

Analysis of Deviance Table (Type III Wald chi-square tests) for the full linear mixed model: Average Respiration ~ Moisture*Dispersal*Origin + (1|sites). Factors significant at $P < 0.05$ are in bold.

	Chi Square	Df	Pr (>Chisq)
Intercept	50.516	1	**<0.001**
Moisture	19.623	1	**<0.001**
Dispersal	2.649	4	0.618
Origin	6.376	2	**0.041**
Moisture: Dispersal	1.161	4	0.884
Moisture: Origin	3.030	2	0.220
Dispersal: Origin	20.950	8	**0.007**
Moisture: Dispersal:Origin	10.835	8	0.211

Table 4 Tukey's HSD posthoc for origin x moisture interaction

Posthoc pairwise comparisons of the one-way ANOVA testing the effect of origin over the 50:50 dispersal treatment mixture proportion for the high moisture data using Tukey's HSD method. Factors significant at $P < 0.05$ are in bold.

Contrast	Estimate	SE	Df	t.ratio	*P*
EE-EW	-1.657	2.276	57	-0.728	0.748
EE-WW	4.500	2.787	57	1.615	0.249
EW-WW	6.157	2.276	57	2.706	**0.024**

Table 5 ANOVA results for microbial biomass linear mixed model

Analysis of Deviance Table (Type III Wald chi-square tests) for the microbial biomass linear mixed model: Microbial Biomass ~ Moisture*Dispersal*Origin + (1|sites). Factors significant at $P < 0.05$ are in bold.

	Chi Square	Df	Pr (>Chisq)
Intercept	12.678	1	**<0.001**
Moisture	3.526	1	0.060
Dispersal	0.744	4	0.946
Origin	0.785	2	0.675
Moisture: Dispersal	1.603	4	0.808
Moisture: Origin	0.023	2	0.989
Dispersal: Origin	2.839	8	0.944
Moisture: Dispersal:Origin	2.454	8	0.964

Figure 1 Experimental Vials

A) Examples of microcosm vials (pictured below during experimental setup). B) Vials stored in racks, some in normal holding configuration with parafilm on top (to right of image) while others have septa caps on in preparation for gas sampling (left).

Figure 2 Diagram of experimental design.

West and east sites are denoted by warm- or cool-colored circles, respectively. Soil from each site and its respective microbial community were combined in three east-east (EE) combinations, nine east-west (EW) combinations, and three west-west (WW) combinations. Those combinations were each mixed at five different levels to simulate different levels of forced dispersal: a 100:0, 85:15, 50:50, 15:85, and 0:100 ratio of soils from each site that made up the combination. Soil moisture was maintained at low (5%) and high (20%) levels to mimic conditions often observed in the western and eastern regions of the gradient. MAP stands for mean annual precipitation.

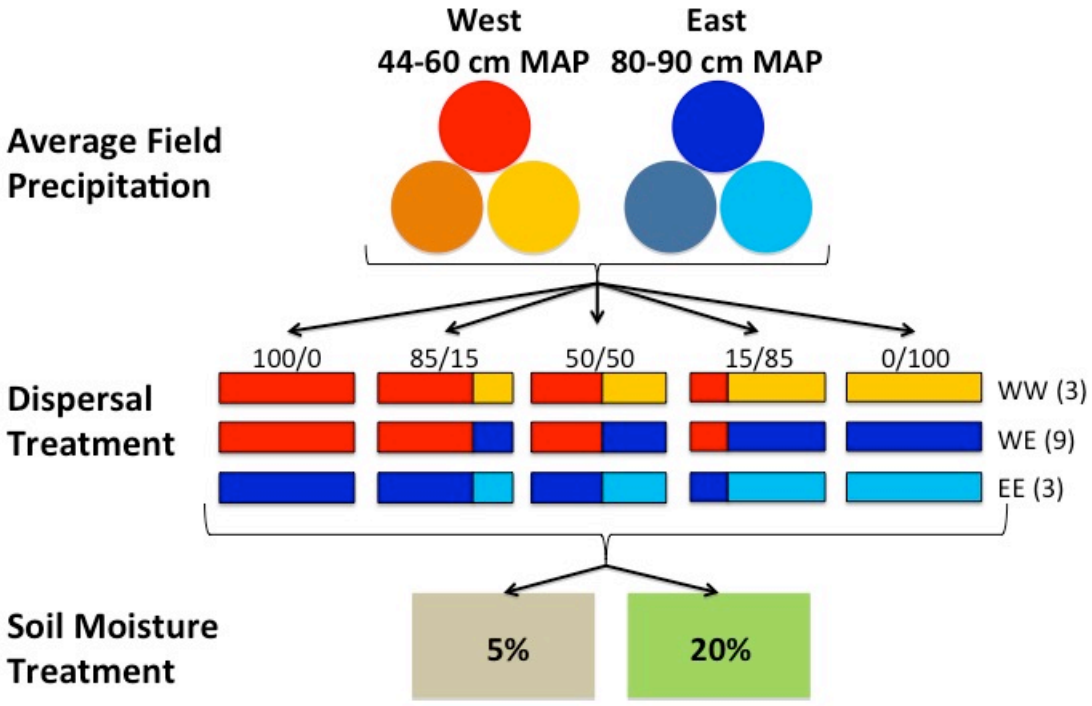


Figure 3 Legacy Respiration East versus West

Mean soil respiration at high and low moisture. Eastern single community microcosms are compared to western single community microcosms. Error bars show ± 1 SE (n = 1196). Respiration response is averaged across all five sampling dates.

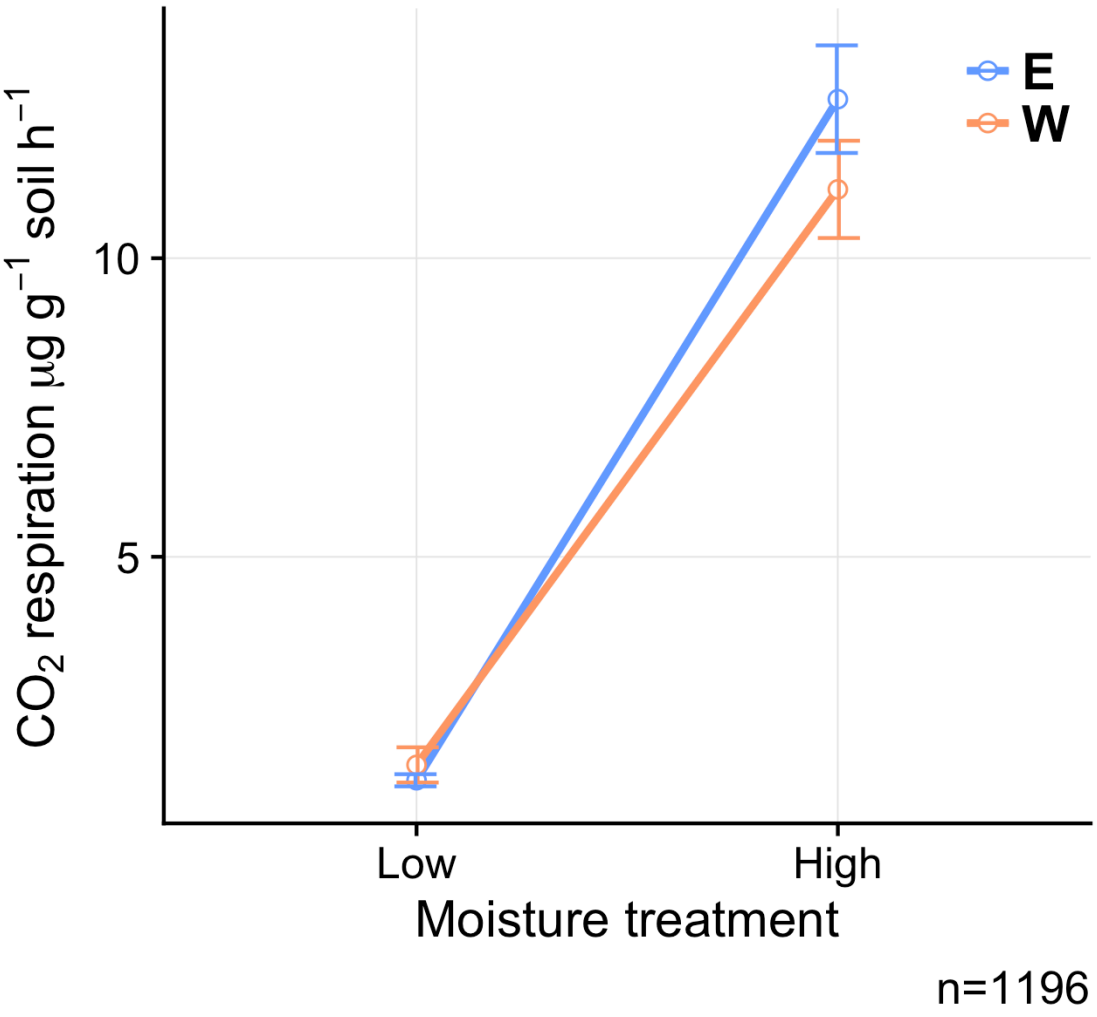


Figure 4 Overall mean soil respiration

Mean soil respiration across (a) east-east sites, (b) east-west sites, and (c) west-west sites by dispersal and moisture treatments. Mixtures 1 and 5 in the east-west origin soils reflect an eastern and western bias, respectively, due to experimental setup. Respiration response is averaged across all five sampling dates. Error bars are ± 1 SE (n = 2984).

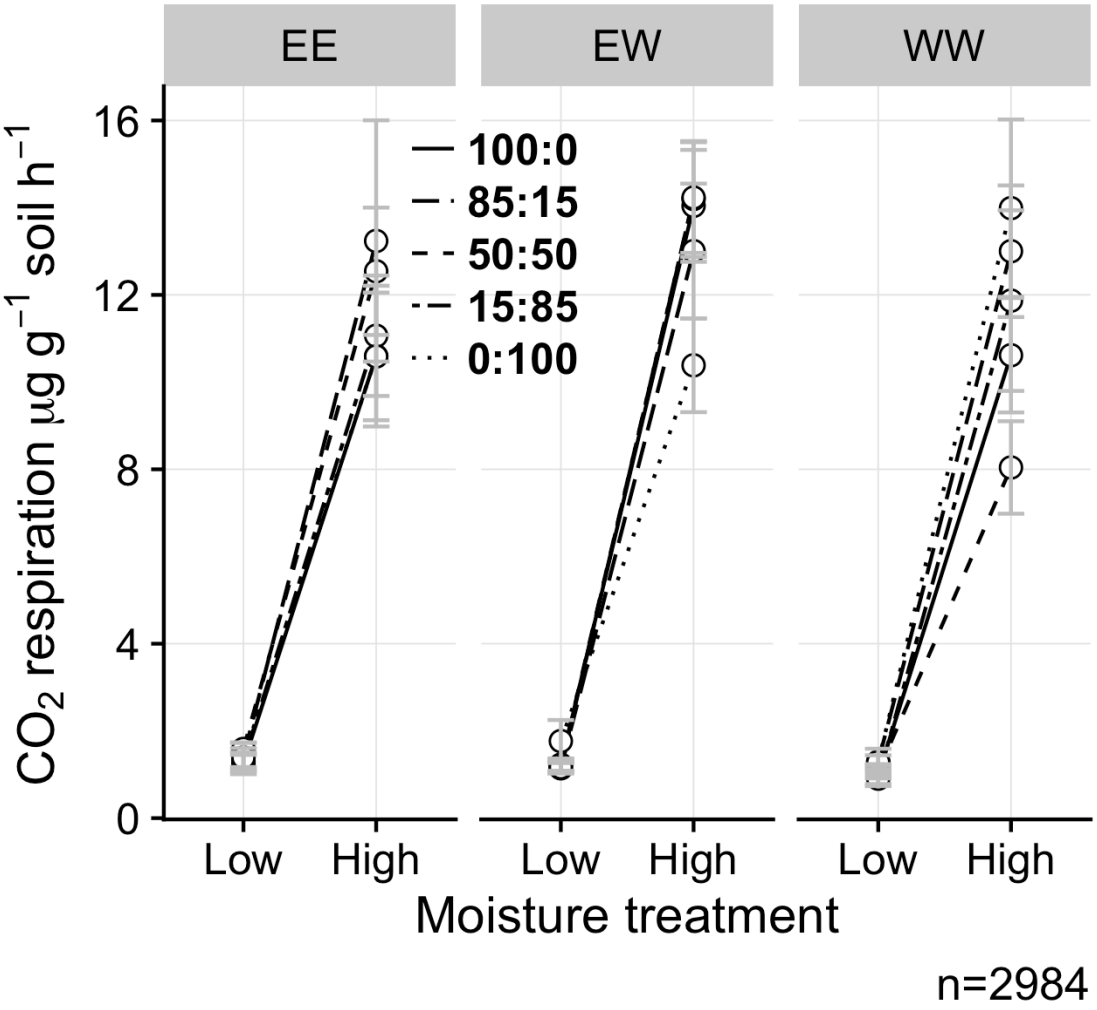
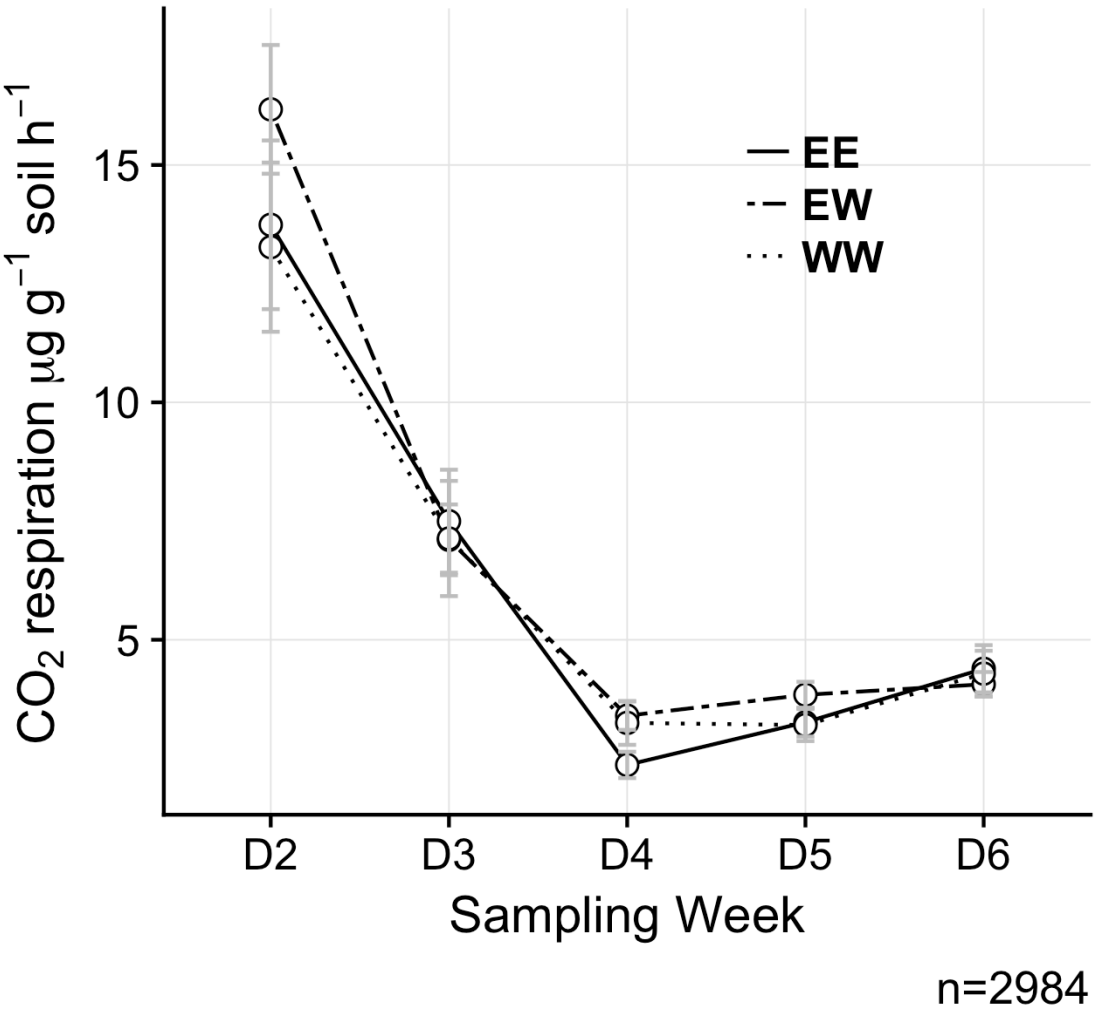


Figure 5 Soil respiration by date

Mean soil respiration for each soil origin treatment across the five sampling dates. Error bars are ± 1 SE (n = 2984).



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